Osteology and myology of the tail in the green snake Opheodrys aestivus (Serpentes: Colubridae): patterns of morphological change

Paul Gritis
Lehigh University

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AUTHOR: Gritis, Paul

TITLE: Osteology and Myology of the tail in the Green Snake Opheodrys Aestivus (Serpentes: Colubridae): Patterns of Morphological Change

DATE: May 31, 1992
Osteology and myology of the tail in the green snake

_Opheodrys aestivus_ (Serpentes: Colubridae):

Patterns of morphological change.

by

Paul Gritis

A Thesis

Presented to the Graduate and Research Committee
of Lehigh University
in Candidacy for the Degree of
Master of Science
in
Biology

Lehigh University

May, 1992
This thesis is accepted and approved in partial fulfillment of the requirements for the Master of Science.

May 5, 1992

Date

Thesis Advisor

Committee
ACKNOWLEDGEMENTS

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This thesis is dedicated to my wife Bea, without whose support and encouragement it would not have been completed.
TABLE OF CONTENTS

Abstract ............................................. 1
Introduction ......................................... 2
Materials and Methods ............................... 4
Results
   Caudal vertebrae ................................. 14
   Caudal muscles ................................. 26
   Sexual dimorphism ............................... 52
Discussion .......................................... 54
Literature Cited ..................................... 61
Vita ................................................. 66
1. Vertebral characters ......................... 19
2. Tail regions of nonlinear size decrease of vertebrae ............. 21
3. States in tail of epaxial muscles of trunk ....... 28
4. States in tail of hypaxial muscles of trunk ....... 39
LIST OF FIGURES

1. Vertebral characters ........................................ 6
2. Selected caudal vertebrae in dorsal view .......... 8
3. Selected caudal vertebrae in lateral view .......... 10
4. Patterns of size decrease in vertebral characters.. 16
5. Plot of distribution of vertebrae 1-100 in males on principal components 2 and 3 ....................... 24
6. Left lateral view of vertebrae 15-27 and associated musculature .............................................. 30
7. Ventral view of basal caudal structures in female .. 36
8. Ventral view of male: A) basal caudal structures, B) origin of retractor penis magnus ......................... 47
9. Model of proposed functional regions of the tail ... 56
ABSTRACT

The tail of *Opheodrys aestivus*, like that of most snakes, appears externally to diminish gradually in size. However, dissection of caudal muscles and morphometric analysis of caudal vertebrae suggests two patterns of size change exist in the tail. Of 16 vertebral measures, five decrease from the beginning of the tail. Most remaining characters increase in size to some point within the first third of the tail before decreasing to the tip. Both multiple range tests and principal components analysis revealed that rate of size change increased significantly for most characters at one or more points in the tail.

The combined features of caudal muscles and vertebrae in *O. aestivus* suggest that three caudal regions may be recognized: a reproductive region (vertebrae 1-50) within which all muscles and reproductive structures are present (some disappear within this region) and where vertebral characters are absolutely largest; a middle region (vertebrae 50 - 80) where vertebrae and muscles typically undergo discontinuous change, and a terminal region (vertebrae 80-100) where vertebral characters and muscles become highly simplified. The first two regions may contribute towards total propulsive effort. The terminal region may serve less for locomotion than for passive misdirection or loss during predation.
INTRODUCTION

The tetrapod tail is a continuation of the axial skeleton, musculature, nerve cord, and integument posterior to the body cavity (Mahendra, '56). Although tetrapods display a bewildering array of tail shapes (e.g. Hickman, '79), the general morphological pattern can be described as a diminution in size. The cross sectional area of the caudal vertebrae and muscles therefore must become progressively reduced along the tail. This might occur in three ways: 1) gradual, continuous reduction, 2) punctuated or discontinuous reduction, or 3) loss of particular elements. Support for these models should be readily obtainable by dissection and analysis of muscles and vertebrae.

In most limbed tetrapods the tail is obviously different from the trunk and most show caudal muscle modifications associated with the hind limbs and pelvic girdle (Haines, '35; Renous, '77). On the other hand, in many limbless squamates the tail is not noticeably different from the trunk, suggesting that the vertebral column and musculature may simply continue unmodified into the tail.

Previous studies of ophidian caudal vertebrae (summarized in Hoffstetter and Gasc, '69; Keiser, '70) have been descriptive and have not considered variation. Quantitative studies of ophidian vertebrae (summarized in LaDuke, '91) have ignored the tail. Descriptions of caudal
muscles in snakes are limited to the early works of d’Alton (1834) and McKay (1890), as most recent work on trunk muscles (e.g., Gasc, ’81; Jayne, ’82) have not included the tail. Reviews of tail morphology and function (Wake,’70; Greene, ’73) have not considered the muscles and vertebrae except for specializations for caudal autotomy.

This study describes the caudal vertebrae and muscles of Opheodrys aestivus, a North American semiarboreal colubrid, selected because its relatively long tail (about 40% of the snout-vent length) may be especially suitable for the study of intracaudal variation. Description of patterns of change in caudal muscles and vertebrae in O. aestivus should contribute toward understanding the general question of packing anatomical structures into an ever-diminishing envelope, and generate testable hypotheses about function of the tail in this species.
MATERIALS AND METHODS

To examine changes in vertebrae along the length of the tail, sixteen measures (Fig. 1) were made on dry skeletons of ten male and ten female adult *Opheodrys aestivus*. In each snake the first and every tenth of the first 100 caudal vertebrae (Figs. 2, 3) were examined. Caudal vertebrae are distinguished from the cloacal series by the presence of at least one fused, unforked pleurapophysis. The left side of the vertebra (in this paper, "vertebra" refers only to caudal vertebra, others are specified "precaudal" or "cloacal") was used for measures of paired structures if undamaged; otherwise the right side was used. The majority of characters (Fig. 1) were taken from Auffenberg ('63) and represent muscle attachment sites (NSH, NSL, PRW), articular facets and joints (COH, COW, POW, PRW, PZL, PZW, ZSW), vertebral length (CEL, NSL, PRPO), width (COW, PRW, ZSW), and height (COH, NAH, NSH). The following measurements differ slightly from those of Auffenberg. Neural spine height (NSH) was measured at the midpoint in lateral view rather than the anterior portion of the spine, because the latter was usually broken. Width across the prezygapophyses (PRW) in this study was measured across the facets only and did not include the accessory processes. Measures of the pleurapophyses (PLD, PLL) and haemal arches (HED, HEL) are new and represent the straight-line length (HEL, PLL) and
Figure 1. Vertebral characters. CEL, centrum length; COH, height of cotyle; COW, width of cotyle; HED, haemal arch depth; HEL, haemal arch length; NAH, neural arch height; NSH, neural spine height; NSL, neural spine length; PLD, pleurapophyseal depth; PLL, pleurapophyseal length; POW, postzygapophyseal width (one facet); PRPO, length between pre- and postzygapophyses; PRW, prezygapophyseal width; PZL, postzygapophyseal length; PZW, width across both postzygapophyses; ZSW, zygosphenial width.
Figure 2. Selected caudal vertebrae (nos. 1, 20, 50, 70, 90, 100) in dorsal view. Scale bar=1 mm.
Figure 3. Selected vertebrae (nos. 1, 20, 50, 70, 90, 100) in lateral view. Scale bar=1 mm.
maximum ventral depth (HED, PLD) of those structures in lateral view.

Measurements were made (nearest 0.01 mm) with electronic digital calipers (Fowler Industries) mounted on the mechanical stage of a dissecting microscope so that movements of the stage relative to an ocular micrometer were recorded. Data were exported (Zubair interface) to a microcomputer (Bentley 286) and the data stored on floppy disk (ASCII) using "Lessoft" software (by Leslie Marcus, American Museum of Natural History). Accuracy of the calipers was monitored with a metric ruler. One specimen was measured twice, at the beginning and end of the study to test for measurement error.

Morphometric data for each character were analyzed for significant differences between vertebral position and sex. Each character was examined for changes along the length of the tail, testing the null hypothesis that all vertebral characters become smaller at the same rate. To determine whether changes in character size changes followed the continuous or the noncontinuous model, multiple range analyses (least significance difference, p<0.05) were performed for each character for each sex.

Rates of change (mm/vertebral interval) for each character were assessed by subtracting the mean minimum value $V_{\text{min}}$ from the mean maximum value $V_{\text{max}}$, dividing by $V_{\text{max}}$, and dividing the result by the interval (number of
vertebrae) separating $V_{\text{max}}$ from $V_{\text{min}}$. In 75% of the cases $V_{\text{max}}$ was located either at vertebra 1 or 10, in no case beyond vertebra 30. Only 2 characters had $V_{\text{min}}$ at positions other than vertebra 100. For one character (POW-females), $V_{\text{min}}$ was at vertebra 90. For another character (HEL- males), $V_{\text{min}}$ was at vertebra 1 and the rate was calculated using the difference between vertebrae 10 and 100.

To assess how all characters contribute to vertebral shape along the tail, principal components analysis (PCA) was performed on each sex separately. PCA was run on SAS, the other tests on Statgraphics version 2.6 (Statistical Graphics Corp.).

Muscle dissections were done under a Bausch and Lomb dissecting microscope at 7-30X. Muscle staining using Weigert's variation of Lugol's Solution (Bock and Shear, '72) was helpful in tracing muscles. Dissections were performed in air. Damp muscles (excess alcohol blotted away) were easier to study than those dissected under alcohol. Prior to study of the caudal muscles, the precaudal musculature of O. aestivus was examined using accounts of colubrid myology (Mosauer, '35; Gasc, '81; Jayne, '82) and was found to agree very well with those accounts. For the purposes of nomenclature, caudal muscles were assumed to be serial homologues of those precaudal muscles with similar attachment points and fiber direction. Muscle terminology follows Gasc ('81), except as noted. The anterior portion
(first 30 vertebrae) of the tail was examined to determine which precaudal muscles continue into the tail. Those muscles present were noted for their attachment points, fiber and tendon lengths, and fiber direction. Those characters and any changes were noted for each muscle at three or more intervals throughout the tail, ending at vertebra 100, to test the null hypothesis that all muscles remain unchanged throughout the length of the tail. Fiber lengths are presented with reference to vertebrae, although data collection usually was done using subcaudal scales. Vertebral and subcaudal numbers agreed within 2%. Drawings were made by coordinate transposition onto graph paper, using an ocular grid micrometer.

Specimens examined: Fluid preserved: DLC (D. Cundall, private collection) 19-21, 51, 55; LU (Lehigh University) 612, 1364-65; 1377-79, 1381, 1383-84; PG (P. Gritis, private collection) 12-19, 25, 28, 52. Skeletal: LSUMZ 9682, 9684-85, 9688-90, 9692-94, 9396; PG 01; 03-08, 10; TCL (Thomas C. LaDuke, private collection) 257.
RESULTS

Caudal Vertebrae

Two general patterns of change were identified. Five characters (NAH, POW, PRW, PZW, ZSW) reflecting primarily of vertebral width, showed essentially linear decrease in size, with the maximum located at the first vertebra (Type I change, Fig. 4a). Type II change is typified by an increase in size in the anterior tail followed by a subsequent decrease (Fig. 4b). Maximum size is achieved at different points for different Type II characters; at vertebra 10 (CEL, COH, COW-males, HED, NSH, PLL); at vertebra 20 (HEL, PRPO-females, PZL-males); and at vertebra 30 (NSL, PLD-males, PRPO-males).

For the remaining three characters, either the sexes are dimorphic or one sex is not readily classified as either Type. For cotyle width (COW) the males show a Type II curve, whereas in females vertebrae 1 and 10 are less different and the curve is not readily identified as either Type. For PLD (pleurapophyseal depth), females are readily classified as Type I, but in males the values for vertebrae 1-10-20 are very similar and the curve is difficult to classify as either Type. Females are readily classified as Type II for pleurapophyseal length (PLL), but males more closely fit Type I.
Figure 4. Patterns of size change in vertebral characters. Graph of mean and standard deviation of A) prezygapophyseal width of females (n=10) showing linear (Type I) reduction; and B) length between pre- and postzygapophyses of females (n=10) showing Type II size change (see text).
The rates of decrease ranged from 0.003-0.020 mm/vertebra (Table 1) and do not differ significantly (T-test, p<0.05) between Types I and II. Type I characters diminish to a significantly smaller percentage of their maximum value than do Type II characters (61% vs. 48%, T-test, p<0.05). The lowest percent decrease (23-49%) was shown by measures of length (CEL, HEL-males, NSL, PLL-males, PRPO, PZL-females), the highest (62-84%) by measures of height and width (HEO, NSH, PLD, PZW-females). On the basis of percent decrease, the characters with the least relative amount of change are measures of vertebral length (CEL, NSL, PRPO), which diminish by 23-39% from the maximum mean value to vertebra 100 (Table 1). The remaining measures of length (HEL, PZL, PLL), all but one measure of width (POW, ZSW, PRW, COW, PZW-males only), and three measures of height (COH, NAH, and HED-males only) show moderate decreases ranging from 41-64%. Maximum diminution (72-84%) occurred in three height measures (NSH, PLD, and HED-females only) and one width measure (PZW-females).

The female sample was significantly larger (2-way ANOVA, p<0.05) than the male sample for all characters except neural spine length (NSL) and postzygapophyseal length (PZL). This correlates with larger adult size reached by females of this species (Grobman, '84) and is assumed not to represent a sampling artifact.
Table 1. Vertebral characters (CHAR), maximum ($V_{\text{max}}$) and minimum ($V_{\text{min}}$) mean values (vertebral number; mean in mm), percent reduction (RED%) of absolute size of listed characters from $V_{\text{max}}$ to $V_{\text{min}}$, rate (mm/vertebra, $V_{\text{max}}$ to $V_{\text{min}}$).

# POW females, where $V_{\text{min}}=\text{vertebra 90}$,

* HEL males, where $V_{\text{min}}=\text{vertebra 1}$ (see text)

Character acronyms given in Figure 1.
<table>
<thead>
<tr>
<th>Females</th>
<th></th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHAR</td>
<td>Vmax</td>
<td>Vmin</td>
</tr>
<tr>
<td>NSL (30, 1.714)</td>
<td>1.305</td>
<td>24</td>
</tr>
<tr>
<td>PRPO (20, 2.874)</td>
<td>1.79</td>
<td>38</td>
</tr>
<tr>
<td>CEL (10, 2.331)</td>
<td>1.421</td>
<td>39</td>
</tr>
<tr>
<td>HEL (20, 1.482)</td>
<td>0.808</td>
<td>45</td>
</tr>
<tr>
<td>PZL (1, 0.6)</td>
<td>0.307</td>
<td>49</td>
</tr>
<tr>
<td>PLL (10, 1.429)</td>
<td>0.674</td>
<td>53</td>
</tr>
<tr>
<td>COH (10, 0.832)</td>
<td>0.387</td>
<td>54</td>
</tr>
<tr>
<td>COW (1, 0.997)</td>
<td>0.457</td>
<td>54</td>
</tr>
<tr>
<td>NAH (1, 0.726)</td>
<td>0.327</td>
<td>55</td>
</tr>
<tr>
<td>POW# (1, 0.566)</td>
<td>0.251</td>
<td>56</td>
</tr>
<tr>
<td>ZSW (1, 1.401)</td>
<td>0.605</td>
<td>57</td>
</tr>
<tr>
<td>PRW (1, 2.528)</td>
<td>0.943</td>
<td>63</td>
</tr>
<tr>
<td>HED (10, 0.711)</td>
<td>0.189</td>
<td>73</td>
</tr>
<tr>
<td>PLD (1, 0.98)</td>
<td>0.263</td>
<td>73</td>
</tr>
<tr>
<td>NSH (10, 0.467)</td>
<td>0.097</td>
<td>79</td>
</tr>
<tr>
<td>PZW (1, 2.404)</td>
<td>0.387</td>
<td>84</td>
</tr>
<tr>
<td>NSL (30, 1.622)</td>
<td>1.251</td>
<td>23</td>
</tr>
<tr>
<td>CEL (10, 2.162)</td>
<td>1.559</td>
<td>28</td>
</tr>
<tr>
<td>PRPO (30, 2.669)</td>
<td>1.846</td>
<td>31</td>
</tr>
<tr>
<td>HEL* (20, 1.39)</td>
<td>0.821</td>
<td>41</td>
</tr>
<tr>
<td>PLL (1, 1.001)</td>
<td>0.542</td>
<td>46</td>
</tr>
<tr>
<td>PZL (20, 0.562)</td>
<td>0.288</td>
<td>49</td>
</tr>
<tr>
<td>CON (10, 0.903)</td>
<td>0.451</td>
<td>50</td>
</tr>
<tr>
<td>COH (10, 0.682)</td>
<td>0.336</td>
<td>51</td>
</tr>
<tr>
<td>ZSW (1, 1.327)</td>
<td>0.617</td>
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</tr>
<tr>
<td>PZW (1, 2.247)</td>
<td>0.924</td>
<td>59</td>
</tr>
<tr>
<td>PRW (1, 2.377)</td>
<td>0.973</td>
<td>59</td>
</tr>
<tr>
<td>POW (1, 0.503)</td>
<td>0.197</td>
<td>61</td>
</tr>
<tr>
<td>HED (10, 0.538)</td>
<td>0.207</td>
<td>62</td>
</tr>
<tr>
<td>NAH (1, 0.718)</td>
<td>0.262</td>
<td>64</td>
</tr>
<tr>
<td>PLD (30, 0.601)</td>
<td>0.171</td>
<td>72</td>
</tr>
<tr>
<td>NSH (10, 0.336)</td>
<td>0.085</td>
<td>75</td>
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</table>
Table 2. Tail regions showing nonlinear size decrease, based upon multiple range tests. Letter (F=female, M=male) denotes nonlinear change for that character at that tail region. VERT=vertebral number. Character acronyms given in Figure 1.
### VERTEBRAL CHARACTERS

<table>
<thead>
<tr>
<th>VERT</th>
<th>CEL</th>
<th>COH</th>
<th>COW</th>
<th>HED</th>
<th>HEL</th>
<th>NAH</th>
<th>NSH</th>
<th>NSL</th>
<th>PLD</th>
<th>PRPO</th>
<th>PZL</th>
<th>PZW</th>
<th>ZSW</th>
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<tr>
<td>1-10</td>
<td>F,M</td>
<td>F,M</td>
<td>F,M</td>
<td>M</td>
<td>M</td>
<td>F,M</td>
<td>M</td>
<td>M</td>
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<td>M</td>
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<tr>
<td>10-20</td>
<td>F</td>
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<td>40-50</td>
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<td>50-60</td>
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<td>M</td>
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<td>60-70</td>
<td></td>
<td></td>
<td>M</td>
<td>M</td>
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<td>80-90</td>
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<td>90-100</td>
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</table>
Multiple range analyses (Least Squares Difference, p<0.05) performed separately for each sex gave the following results (Table 2). Three characters (PLL, POW, PRW) showed only gradual linear decrease. The remaining characters showed some discontinuous change along the tail. Eight of these departed from linearity at only one vertebral region, and two at two nonsuccessive regions. The remaining three characters each showed discontinuous change at four regions. In only one instance did these three characters change at the same vertebral position (vertebrae 10-20, females only). For two characters the male sample changed at the same region (vertebrae 60-70 for COH and COW; vertebrae 80-90 for COH and ZSW). In only four cases did both sexes change for the same character (CEL, COH, HED, NSH) at the same region (all at vertebrae 1-10).

Further evidence of discontinuities was provided by principal components analysis. A plot of principal components 2 and 3 yields a discontinuous curve, especially notable for vertebra 60 and 70 (Fig. 5), in contrast to the smooth curve expected for continuous change.

The multiple range tests provided rankings of vertebral number by absolute size for each character. The set of 16 characters and 2 sexes yielded 23 different rankings, most of which were represented by a single character. The most common ranking was that in which vertebrae were sequentially ranked with vertebra 1 the largest and 100 the smallest.
Figure 5. Plot of distribution of vertebrae 1-100 in males (n=10) on principal components 2 and 3.
(Type I reduction). Other rankings usually differed by placement of only a single vertebra, usually vertebra 1.
Caudal muscles and nonosseus connective tissue

Epaxial series.--The dorsal epaxial musculature of the trunk extends with only minor modifications into the tail (Table 3). The M. transversospinalis and longissimus dorsi groups (Gasc, '81) continue into the tail and have segments with attachments in both precaudal and caudal regions. Segmental and tendon lengths decrease for all muscles which in the trunk span more than two vertebrae. In the dorsalmost unit of the transversospinalis, the tendon of origin of the semispinalis is continuous with the dorsal tendon of the tendinous arch of the longissimus dorsi (Fig. 6). Posteriorly in the tail, the tendon of origin and the dorsal branch of the tendinous arch become very reduced and were not found caudal to vertebra 75.

The spinalis in the tail is arranged as in the trunk. The tendon of insertion of the spinalis-semispinalis segments originating on the first 15 caudal vertebrae span 16 vertebrae, the same number as precaudally (Jayne, '82). Muscles originating posterior to this have shorter tendons. By vertebra 20 they extend over 12-13 vertebrae, by vertebra 75, about five to six vertebrae, by vertebra 80, four to five.
Table 3. States in tail of epaxial muscles of the trunk.
States: 0=absent, 1=present but modified from state in the trunk, 2=essentially unmodified from state in trunk, ?=problematic identification.
<table>
<thead>
<tr>
<th>Muscle</th>
<th>State in tail</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Epaxial:</strong> M. transversospinalis group</td>
<td></td>
</tr>
<tr>
<td>semispinalis      SSP</td>
<td>1</td>
</tr>
<tr>
<td>spinalis          SPI</td>
<td>2</td>
</tr>
<tr>
<td>interarticularis superior IAS</td>
<td>2</td>
</tr>
<tr>
<td>intervertebrales  INV</td>
<td>2</td>
</tr>
<tr>
<td>multifidus        MFS</td>
<td>2</td>
</tr>
<tr>
<td><strong>M. longissimus group</strong></td>
<td></td>
</tr>
<tr>
<td>longissimus dorsi LOD</td>
<td>1</td>
</tr>
<tr>
<td><strong>M. iliocostalis group</strong></td>
<td></td>
</tr>
<tr>
<td>iliocostalis      ILC</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 6. Left lateral view of vertebrae 15-27 and associated musculature. Each muscle shown is repeated upon each caudal vertebra. Abbreviations: IAS, interarticularis superior; ICT, intercostotransversales; ILC, iliocostalis; INV, intervertebrales; LOD, longissimus dorsi; MFS, multifidus; SPI, spinalis; SSP, semispinalis; TRC, transversus caudae. The length of the anterior tendon of the spinalis has been shortened by 9 vertebrae.
The attachment points of the interarticularis superior (Fig. 6) are similar to those in the trunk. The ventral tendon of origin also receives many muscle fibers from the longissimus dorsi. The ventral tendon could not be found beyond vertebra 70. The dorsal tendon often receives fibers from the overlying multifidus before the fibers of the interarticularis itself appear. There is much intermingling of fibers with those of the adjacent longissimus dorsi such that posterior to about vertebra 80, the interarticularis superior cannot be distinguished from fibers of the longissimus dorsi. The intervertebralis and the multifidus (Fig. 6) are arranged as in the trunk. The latter muscle remains relatively wide; at vertebra 70 it may be about three times as wide in lateral view as the anterior tendon of the neighboring spinalis.

The interarticularis inferior was not identified in the tail. In the trunk, it originates in common with the longissimus dorsi, upon the accessory process, and extends cranially to insert partly upon a rib head and also to join with fibers of the levator costae. In the tail, fibers were found associated with the ventromedial face of the longissimus dorsi tendon. At vertebra 25, these fibers have a diffuse, fleshy origin upon the accessory process and pleurapophysis near vertebra 22. However, because these fibers do not have a common attachment with the longissimus dorsi and do not attach to a rib head, they may not be
homologous with the interarticularis inferior but may simply be part of the longissimus dorsi. The absence of the interarticularis inferior in the tail may be associated with the absence of the levator costae and the ribs.

The longissimus dorsi (Fig. 6) arises, as in the trunk, by pinnate attachment via a short, strong tendon to the accessory process. Muscle fibers in the anterior tail approach the process quite closely, resembling a fleshy attachment; caudally, the attachment is less fleshy.

Anteriorly in the tail the tendinous arch is similar in form to that in the trunk, spanning from one to two vertebrae. More posteriorly in the tail the arch becomes narrower and longer, and may span two or three vertebrae, decreasing to slightly less than one by vertebra 86. A thin sheet of dense connective tissue (the "membranous fan" of Gasc, '81) passes medially from the arch and attaches to the vertebra. In the anterior tail, the dorsal tendon extends two to three vertebrae, the ventral tendon about five. By vertebra 80, the arch still spans one to two vertebrae, the ventral tendon two to three. For the caudalmost segment of the longissimus dorsi examined, arising from vertebra 86, the arch was slightly less than one vertebra long and the ventral tendon about three. The dorsal branch of the arch becomes greatly reduced near vertebra 70, as does the associated tendon of the semispinalis.
The muscular portion of the longissimus dorsi is four to six vertebrae long anteriorly in the tail, and by vertebra 86 only two to three. Further caudally, fewer muscle fibers approach the insertion. There is much intermingling of fibers between adjacent segments of the longissimus dorsi, as well as with other muscles. This tendency increases posteriorly in the tail.

The iliocostalis (Fig. 6) arises, as in the trunk, via a long tendon continuous with the ventral portion of the tendinous arch of the longissimus dorsi. The tendon extends over six to eight vertebrae (about four by vertebra 75). The anterior tendon extends over four to six vertebrae and inserts on the posterior edge of a pleurapophysis. Each segment has only a single muscle belly. In the trunk each segment has two bellies separated by an intermediate tendon. In the tail, the belly extends over four to six vertebrae, becoming progressively shorter posteriorly, to about two by vertebrae 75. There is extensive intermingling of fibers between adjacent segments of this muscle. In no case could an "individual" segment be isolated. The anterior and posterior tendons are extensively connected to neighboring tendons throughout their length. When a single tendon is pulled laterally, numerous tendinous strands are observed to be continuous with adjacent tendons. Many strands also attach to the superficial fascia. These are readily seen when the fascia is removed. Also, the anterior tendon
usually joins that of the preceding iliocostalis, forming a large "compound" tendon from several consecutive segments. The anterior tendons form much of the superficial ventral layer of connective tissue, and they also attach to tendons of the suprapleuratapophyseus (Figs. 6 and 7). The iliocostalis in the tail has been called the flexor caudae superficialis (Hoffmann, 1890), but the highly distinctive attachment to the longissimus dorsi is here considered sufficient to establish homology with the precaudal muscle.
Figure 7. Ventral view of basal caudal structures in female Q. aestivus. CLO, cloaca; CSA, constrictor sacculi ani; HAE, haemal arch; RCL, retractor cloaca; SAC, cloacal sac; SCA, constrictor sacculi ani; SCS, subcaudal scales, reflected; SHE, midventral tendinous sheath; other abbreviations as in Fig. 6. The right and part of the left RCL have been removed to show the right CSA and SAC. The cranial portion of the fused RCL is shown anterior to SHE.
Hypaxial series

Medial layer.--None of these trunk muscles was identified in the tail (Table 4). A single muscle, the intercostotransversales, which may be homologous to a portion of the intercostalis, is described in the following section.

Lateral layer.--In this layer of the trunk there are 11 muscles present (Table 4), all of which have at least one attachment to a rib. Only the following two muscles are present in the tail.

The muscle fibers extending longitudinally between successive pleurapophyses are the intercostotransversales (Fig. 6). Similarly arranged fibers between adjacent ribs in the trunk represent the intercostalis group (Table 4). They are present between cloacal lymphapophyses, and continue onto the pleurapophyses. The last lymphapophysis has fibers present for the proximal half of its length, coinciding with the shorter pleurapophyses. Unlike the trunk, muscle layers with differing fiber direction were not found in the tail. Many fibers of this muscle diverge laterally to attach to the posterior tendon of the suprapleurapophyseus. The intercostotransversales gradually decrease in volume posteriorly, in accord with a progressive anterior shift of the pleurapophyses and concomitant reduction in the amount of available attachment space. There are few if any fibers remaining by vertebra 70,
Table 4. States in tail of hypaxial muscles of the trunk. States: 0=absent, 1=present but modified from state in the trunk, 2=essentially unmodified from trunk, ?=problematic identification.
### Hypaxial: Medial layer

<table>
<thead>
<tr>
<th>Muscles</th>
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</thead>
<tbody>
<tr>
<td>intercostalis internus (brevis et longus)</td>
</tr>
<tr>
<td>obliquus internus (pars dorsalis et ventralis)</td>
</tr>
<tr>
<td>transversus abdominis dorsalis</td>
</tr>
<tr>
<td>transversus abdominis ventralis</td>
</tr>
</tbody>
</table>

### Lateral layer

<table>
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<tbody>
<tr>
<td>costocutaneous inferior CCI</td>
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<tr>
<td>costocutaneous superior CCS</td>
</tr>
<tr>
<td>costo-vertebro-costalis CVC</td>
</tr>
<tr>
<td>interarticularis inferior IAF</td>
</tr>
<tr>
<td>intercostalis externus ICX</td>
</tr>
<tr>
<td>intercostalis quadrangularis ICQ</td>
</tr>
<tr>
<td>intercostalis ventralis ICV</td>
</tr>
<tr>
<td>levator costae LEV</td>
</tr>
<tr>
<td>supracostalis lateralis inferior SLI</td>
</tr>
<tr>
<td>supracostalis lateralis superior SLS</td>
</tr>
<tr>
<td>tuberculocostalis TBC</td>
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</tbody>
</table>

### Subvertebral

<table>
<thead>
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<th>Muscles</th>
</tr>
</thead>
<tbody>
<tr>
<td>parapophyso- hypapophyseus PPH</td>
</tr>
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</table>
and those fibers present may actually belong to the overlying suprapleuratophyseus or longissimus dorsi. This muscle corresponds topographically to the precaudal intercostalis series. Only a single layer is present in the tail and cannot be assigned to any of the three precaudally. The homology of pleurapophyses and ribs not being established (Hoffstetter and Gasc, '69), the name proposed by Hoffmann (1890), intercostotransversales, is used here.

The long muscle with attachments upon pleurapophyses is the suprapleuratophyseus (Figs. 6 and 7). The tendon of origin arises from the cranialateral face of the tip of a pleurapophysis, and passes cranially over two to three vertebrae where the belly arises. Posterior to vertebra 60, the tendon is about one to two vertebrae in length. The tendon of insertion is one to two (usually one) vertebrae long and attaches to the caudal surface of a pleurapophyseal tip. Anteriorly, the belly extends over four vertebrae (by vertebra 60 only about one vertebra) and is ventromedial to the adjacent iliocostalis. The suprapleuratophyseus appears to be almost undifferentiated into discrete segments, and shows extensive intermingling of muscular and tendinous fibers (Fig. 6). A similar condition was noted for the obliquus externus profundus and supracostalis lateralis superior (Gasc '81). The tendon of origin often bifurcates and receives muscle fibers from adjacent segments, as well as from the intercostotransversales. This muscle was
previously called the flexor caudae superficialis (Hoffmann, 1890). It is likely the homologue of one of the supracostals (Table 4). The relationship of the ribs and pleurapophyses being unknown, the muscle is here called the supracleurapophyseus.

Precaudal subvertebral series.—No serial homologues of these muscles extend into the tail of *Q. aestivus* (Table 4). The subvertebral muscles present caudally are described in the following section.

Muscles unique to the tail.—The following caudal hypaxial muscles have no obvious serial homologues in the trunk: intercostotransversales, supracleurapophyseus, constrictor sacculi ani, retractores cloacae, retractor penis magnus, transversus caudae.
Basal caudal and hemipenial muscles, nonosseous connective tissues, cloacal sacs, and hemipenes

The cloaca is separated from the caudal region by a thick transverse septum composed, in part, of cloacal musculature and connective tissue. The caudal surface of the septum serves as the attachment point for some of the muscles described later.

Immediately beneath the skin, the caudal muscles are covered with a superficial fascia, through which can be seen the muscle groups and their tendons, very much as noted by Gasc ('81) for colubrid trunk muscles. No cutaneous muscles occur in the tail. Following removal of the fascia, the following structures are seen in ventral view.

Running longitudinally along the ventral midline, and visible through the superficial fascia, is a complex of both loose and dense connective tissues, including long tendons. At the base of the tail the complex is thin and easily torn. Further caudally, around the sixth vertebra, the connective tissue invests the tendons of the suprapleurapophyseus and iliocostalis. Those muscles, described earlier, originate caudally and pass cranially and ventrally over the cloacal musculature to their insertions in the trunk. This longitudinal complex of tendons and loose connective tissue forms a midventral sheath ("mittleren aponeurosis oder weisse linie" of d'Alton, 1834:534) that serves, in part, to unite the lateral walls of axial muscles on either side.
(Fig. 7). The lateral boundaries of the sheath are comprised of compound tendons formed by the confluence of tendons of the iliocostalis and suprapleuralapophyseus. The compound tendons are broader than the constituent ones. This sheath has no attachment to the subcentral surfaces or to the haemal arches of the vertebrae although some muscles attach to it.

The muscle most superficial to the midventral sheath posterior to the cloaca is the transversus caudae (Figs. 6 and 7) which has two points of origin. Most fibers arise from a subvertebral aponeurosis lateral to the haemal arches, others attach to the dorsal portion of the arches. The aponeuroses of each side do not contact each other. Other fibers originate upon tendons of the medial layer of intermingled iliocostalis-suprapleuralapophyseus. There are two points of insertion: those fibers nearest the cloaca attach to the caudal edge of the postcloacal septum, but most insert onto the midventral sheath. A few fibers attach to the associated tendons of the iliocostalis or suprapleuralapophyseus. The insertion, particularly along the midventral sheath, is very weak and readily destroyed. At the base of the tail, fibers from the left and right halves of this sheet are continuous or nearly so; within one to two vertebrae the fibers become separated by the midventral sheath from the fibers of the opposite side.
The transversus caudae is thickest cranially, becoming thinner caudally. It extends from the base of the tail to about vertebra 15 in females and 40-42 in males. In both sexes it becomes quite reduced caudally, its position being replaced gradually by sheets of obliquely (and some longitudinally) directed fibers, forming superficial lateral muscular walls, the combined suprapleuralapophyseus and iliocostalis. The transversus caudae surrounds the cloacal sacs and the retractores cloacae in both sexes, and also the hemipenes in males. It is the most superficial muscle ventrally and also the dorsalmost of those attaching subvertebrally. The transversus caudae is not found in the trunk although its origin resembles that of the transversus abdominis pars dorsalis which inserts upon the ribs (Gasc, '81). Fusion of the latter muscle with the adjacent transversus abdominis pars ventralis could yield a transverse sheet resembling the transversus caudae. The transversus caudae has been called the transversus penis (McKay, 1890) or propulsor sheet (Beuchelt, '32; Dowling and Savage, '60). Because it is present in both sexes in O. aestivus, those terms are here replaced by the transversus caudae (Ludicke, '62).

The retractores cloacae (Figs. 6 and 7) are paired longitudinal muscles that are partly fused posteriorly. Fibers arise via a fanlike tendon from the subcentral surface and to a lesser extent from a haemal arch near
vertebrae 15-20 in females and 30-35 in males. Other fibers arise from tendons of the iliocostalis and suprapleurapophyseus and diverge medially to join the main group of fibers. The ribbonlike tendon inserts partly onto the postcloacal septum and the ventromedial base of the column formed by the joint attachment of the cloacal sacs and the constrictor sacculi ani (see below and Fig. 7). This column attaches directly to the caudal part of the cloacal septum. In males the components of this column, superficial to deep, are the retractor cloaca, hemipenis, cloacal sac and constrictor sacculi ani (Fig. 8A). The retractor cloaca extends cranially from the origin and in males, passes ventrally over the hemipenes and hemipenial muscles. Usually the paired bundles align at the midline and share some fibers but the connection is weak and can be separated readily. There is some attachment of muscle fibers to the midventral sheath, the combined iliocostalis-suprapleurapophyseus and the transversus caudae, especially at this point of fusion. In males each bundle remains clearly associated with the ipsilateral hemipenis, and there is some sharing of fibers with the retractor penis magnus. The retractor cloaca is small in cross-section, only about one fifth that of the retractor penis magnus in males. This muscle is not found precaudally, and agrees with that described by Hoffmann (1890). This muscle was not mentioned by Dowling and Savage ('60) but may be identical to their
Figure 8. A) Ventral view of basal caudal structures in male *O. aestivus*. Superficial structures removed from the right side to show cloacal sac. B) Origin of retractor penis magnus. HP, hemipenis; RPM, retractor penis magnus; others as in Figure 6.
rectus caudae. This remains unverified because those authors did not describe or figure the latter muscle.

The cloacal sacs are surrounded by the constrictor sacculi ani (Fig. 7), which has three distinct points of origin. Most fibers originate subvertebrally. A few arise from the thin connective tissue sheet supporting the cloacal sac. These fibers run obliquely caudoventrally, forming a sling around the sac. There are two additional populations of fibers, ventral and medial. The former pass ventrally over the sac, with some fibers mingling with those of the muscular sling and with the medial population of fibers. All three fiber groups fuse at the caudal end of the sac and are joined by a tendon (or tendonlike structure) extending from the tip of the sac about one to two subcaudals. The combined muscles extend posteriorly, tapering to a fleshy origin, generally involving two or three vertebrae, near vertebra 12. Some fibers attach to lateral faces of haemal arches, and others attach to medial tendons of the iliocostalis- suprapleuralapophyseus complex, but most attach to the subvertebral aponeurosis lateral to the haemal arches. All fiber bundles insert upon the caudal face of the cloacal septum in common with the sac and the retractor cloaca.

The bundles of the constrictor sacculi ani in Opheodrys are assumed to represent the muscle of the same name described by Dowling and Savage ('60). Hardy ('72) stated
that both an "anterior" and "posterior" constrictor sacculi
ani occur in females of another colubrid. Because these
were neither described nor figured, their relationship to
the fibers observed in *Opheodrys aestivus* is difficult to
evaluate.

The bundles of the retractores cloacae overlap, but do
not attach to, the ventral and medial surfaces of paired
tubular structures, the cloacal sacs. The sacs are large
and readily visible, in females about as thick as the
retractor cloaca, extending from the cloacal septum to
about vertebrae five to six in females, and to about
vertebrae two to three in males. They lie just lateral to
the haemal arches. In males the sacs lie dorsal to the
hemipenes. Dorsomedially each sac is supported by a
subvertebral sheet of loose connective tissue. The walls of
the sac become continuous with the cloacal septum.

The caudal subvertebral muscles are not identifiable on
the basis of attachment points or topography as homologues
of precaudal muscles. There is a major organizational
difference between precaudal and caudal subvertebral
muscles. In the trunk, each vertebra serves as a point of
origin and insertion for each muscle, and the muscles are
segmentally repeated. One segment of any muscle does not
span the greater portion of the trunk. No precaudal muscles
attach only to two widely-spaced vertebrae, passing over
several others without attachment. In the tail, there are
fewer subvertebral muscles and they span greater numbers of vertebrae. Many caudal vertebrae do not serve as attachment points for some subvertebral muscles. Caudal subvertebral muscles usually spread their attachments over more than one vertebra. They are not metameric and each is represented in the tail by only one unsegmented pair.

The hemipenis and its relation to basal subvertebral and hemipenial muscles.--The hemipenes have the same spatial relation to the transversus caudae as do the cloacal sacs in the female, being closely surrounded by that sheet. The medioventral surface of each hemipenis is partly covered by the retractor cloaca, which inserts via a strong flat tendon medial to the base of the ipsilateral hemipenis (Fig. 8A). That muscle has a somewhat different insertion in females, being associated with the cloacal sac, and is more ventral in position (Fig. 7).

The hemipenes have their cranial attachment to the cloacal-caudal septum, from which they extend dorsolateral to the retractor cloaca and ventral to the cloacal sac (Fig. 8A). The fascia covering the hemipenes bears much melanin, even medially, and this melanin is present even when the fascia elsewhere is mostly unpigmented. The hemipenes lie lateral to the haemal arches and do not attach to them, although they are likely in contact during life. Measures of everted and retracted hemipenes yield the same result for hemipenial length, about six to seven vertebrae.
The retractor penis magnus originates (Fig. 8B) primarily via a strong but short tendon from the side of one haemal arch, usually around vertebrae 39-43. The tendon attaches for most of the length of the arch, and the length of the tendon is the width of the haemal arch. Beginning around vertebra 30 there is additional attachment of fibers to the lateral face of a few haemal arches. The muscle runs just lateral to the haemal arches. Left and right portions of the retractor penis magnus are quite distinct at their origin and throughout their length, with minimal sharing of fibers medially. Each makes a fleshy insertion onto the caudal tip of the ipsilateral hemipenis, near vertebra six.

Although no distinct retractor penis parvus was found in Q. aestivus, muscle fibers were observed corresponding approximately to the position noted in other species (Dowling and Savage, '60). Because those fibers had similar relationships to the cloacal sacs in both sexes, they are considered part of the constrictor sacculi ani in Q. aestivus. The retractores cloacae in males insert partly onto the medial and dorsal surfaces of the hemipenial base.
Sexual dimorphism in caudal structures.--A number of caudal structures differ in size or shape between the sexes in *Opheodrys aestivus*. All vertebral characters in this study were significantly larger in females (2-way ANOVA, p<0.05) except for NSL and PZL. In addition, the haemal arch tips of most anterior vertebrae are in contact in adult males but not in females (Keiser, '70), a feature obvious by direct observation, but not detectable from the 16 morphometric variables. Among males examined here, the first few haemal arch tips are usually not in contact (range: vertebrae 1-7, mean=3) and contact terminates at vertebra 20-41 (mean=32). Muscle attachment points were not verified for these specimens, but in others the origin of the retractor penis magnus occurs further caudally, near vertebra 45.

Dimorphism was observed in all caudal subvertebral muscles except for the constrictor sacculi ani. The transversus caudae extends to about vertebra 15 in females, and to 40-42 in males. The retractores cloacae in females extend to vertebrae 15-20 and in males from 30-35.

The cloacal sacs in females range from 3-5.5 vertebrae in length, in males from 1.5-4. In some animals (40%) the left and right sacs are equivalent in length (number of vertebrae), in others either the left (50%) or right (10%) may extend further caudally, up to about one vertebrae, than the other. In males, most (75%) had sacs equivalent in length, whereas in most females (80%) the left sac extended
further caudad than the right. No trace of hemipenes or hemipenial muscles was found in females in this study, although such structures have been reported for other colubrids (Hardy, '72).
DISCUSSION

The tail of *Q. aestivus* contains fewer elements, especially in the hypaxial portion, and has an overall simpler arrangement than does the trunk. Size decrease in vertebrae is accomplished by Types I and II reduction, and within each Type by continuous and discontinuous reduction. Discontinuous reductions, identified by the multiple range analysis, were concentrated between vertebrae 60-100. Discontinuous decrease in vertebral size coincides with both muscular reduction (spinalis-semispinalis and longissimus dorsi) and loss (intercostotransversales and interarticularis superior). The nonmetameric (and therefore unique) subvertebral muscles (retractor cloaca, retractor penis magnus) do not extend to this level.

These morphological observations suggest that the tail of *Q. aestivus* may be divided into three regions (Fig. 9). The first extends from vertebrae 1-50 and includes those values of maximum absolute size for each vertebral and myological character. All caudal muscles and reproductive structures are present in this region and most of the subvertebral muscles do not extend beyond it. The second region extends from vertebrae 50-80. Vertebral characters become further reduced in all dimensions, especially in width and height, and muscles reduce in segmental lengths but maintain the general arrangement as observed in the first region. The third region extends from vertebra 80 to
Figure 9. Model of proposed functional regions of the tail of *O. aestivus*. The levels of vertebrae 50 and 80 are indicated. EXP, expendable region of the tail; LOC, locomotor region; REP, reproductive region. Stippled area represents overlap of locomotor and expendable regions.
the tail tip. In this region characters become highly reduced and some muscles disappear. Because vertebrae were only sampled at intervals of 10, and because there is overlap between the second and third regions in the points of disappearance of some muscles, the proposed model is acknowledged as a simplification. However, the model is useful for discussing the possible functional role(s) of the tail in this species and with modification may serve as a model for the tails of other snakes.

The colubrid tail serves a number of biological roles. Its base houses the cloacal sacs and the hemipenes. The whole tail may be actively moved during feeding or defensive actions (Greene, '73, Henderson, '84) and can form lateral bends similar to those formed in the trunk during lateral undulation. Muscular control of the tail may aid in positioning the cloaca and hemipenis during coitus (Gillingham '79). Additional functional roles have not been proposed previously for the tail in *Q. aestivus* but some are proposed here.

The relatively long tail in *Q. aestivus*, like that in arboreal snakes generally, may result simply from selection for elongation of the body. Attenuation of the trunk may be adaptive if it results in a reduction of body mass, which should increase the amount of thin branch habitat available to an arboreal snake. A relatively long and thin body should also increase the distance capable of being bridged
by the snake when crossing gaps, as well as minimize the muscular force necessary to support the extended portion. The basic pattern of a high tendon:muscle ratio in snake axial muscles may be important in this regard. Snakes with attenuate body form may form a guild (sensu Root, 1967; the resource in this case being habitat) within the aboreal niche, in contrast to heavy-bodied prehensile tailed species.

Arboreal snakes may benefit from a prehensile tail capable of supporting the total body mass. Prehensile tails occur in many arboreal snakes, especially pythons, boids, and viperids, which tend not to show the vine-like elongation of Opheodrys. The tail of O. aestivus can form loose coils and does not seem to be used as an anchor (pers.obs.). It has not been described by other workers as prehensile. Caudal prehensility may require, at the least, extensive development of the hypaxial musculature and a shift in zygapophyseal orientation from horizontal to nearly vertical. The former might compromise the reduction of muscle mass associated with body attenuation, and the latter might reduce lateral flexion. Therefore it is predicted that vine-like arboreal snakes will tend not to have prehensile tails.

The long tail of O. aestivus may serve roles in crypsis and defense against predators. It may simply represent an extension of the trunk which is itself undergoing strong
selection to mimic thin vegetation. When crypsis fails, green snakes will rapidly flee (in the case of human predators). In general, if an escaping snake moves headfirst away from disturbance, its tail will be positioned closest to the predator and may sustain the highest incidence of attacks. This does not involve defensive displays and may simply be referred to as "passive misdirection" of predator attention away from the critical head and anterior body towards the tail tip. Although the entire tail is not expendable because of the reproductive structures present basally, the terminal portion might be. In this case it could be expected that the terminal tail be reduced in size, complexity, and functional importance to minimize its loss. One might also expect structural modification to maximize susceptibility to mechanical breakage. However, evolution of caudal autotomy in snakes may have been constrained by retention of the complex epaxial musculature.

A long tail in itself may be adaptive in lieu of modifications such as caudal regeneration, because the number of attacks sustained might be a function of total tail length (Henderson, '84). Loss of tail tips is common in *O. aestivus* (25-29%, Grobman, '84) as in colubrids generally (Willis et al '82, Broadley, '87) and is likely due primarily to predation.

The tail may also function as an extension of the trunk.
during locomotion. Vertebral articulations and epaxial muscle attachments, which on the basis of topography (Mosauer, '35) and EMG studies (Jayne, '88) are important in lateral undulation, are retained throughout most of the first two caudal regions. The functions of these elements presumably are similar to those of their serial homologues in the trunk.

Lateral flexion is important for locomotion in snakes and presumably for copulation as well. However, in Thamnophis sirtalis fitchi, a terrestrial colubrid snake, loss of as much as two-thirds of the tail is not in itself fatal and results in a decrease in locomotor speed of only 4.5% (Jayne and Bennett, '89). The third caudal region possesses similar musculature, which is however further reduced in length and cross sectional area. This region is capable of lateral and dorsoventral flexion, but because of its absolutely smaller cross sectional area is expected to produce less force.

The caudal vertebrae and musculature may become so reduced posteriorly that they make a negligible contribution to locomotion. The tail might contribute to lateral undulation without being essential for that role and with its relative contribution decreasing posteriorly. In Opheodrys, the major role of the posterior third of the tail may not be locomotory but rather antipredator in nature.
Literature Cited


Willis, L., S.T. Threlkeld and C.C. Carpenter. (1982) Tail loss patterns in Thamnophis (Reptilia:Colubridae) and the
VITA

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Selected refereed publications:

(with S.A. Brunner)

1990b. Variability and significance of parietal and ventral scales in the marine snakes of the genus Lapemis (Serpentes: Hydrophiidae), with comments on the occurrence of spiny scales in the genus.
(with H.K. Voris)

END OF TITLE